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Biology and behavior of a larch bud moth, *Zeiraphera* sp., in Alaska

Richard A. Werner¹

IND/STA

Abstract

A possibly new species or subspecies of larch bud moth of the genus *Zeiraphera*, closely related to *Z. improbana* (Walker), was found associated with tamarack, *Larix laricina* (Du Roi) K. Koch, stands in interior Alaska. An outbreak occurred during 1975 and 1976 over an area of 240 000 ha (590,000 acres). Adult moths were mottled grayish in appearance. First instars emerged from the overwintering egg stage from mid-late May and began feeding as soon as the tamarack buds began to unfold. Pupation, adult emergence, and oviposition occurred from mid-June to mid-July and there was one generation per year. Defoliated tamarack stands turned reddish-brown color by mid-June as partially defoliated needles turned brown, but stands refoliated by mid-July. Parasites and disease killed 99.6 percent of the pupal stage in 1976.

KEYWORDS: Larch bud moth, *Zeiraphera* sp., tamarack, *Larix laricina*, defoliation, biology and behavior, Alaska (interior).

Introduction

An unidentified species or subspecies of bud moth, *Zeiraphera* sp., completely defoliated 142 000 to 240 000 ha of tamarack *Larix laricina* (Du Roi) K. Koch, during 1975 and 1976 in the Tanana River drainage near Fairbanks, Alaska (Rush et al. 1977). The area infested extended from Tok (near the Canadian border) west to Nenana and from Fairbanks south to the Alaska Range (fig. 1). An infestation by *Zeiraphera* apparently occurred throughout the same area in 1958² as extensive areas of tamarack were heavily defoliated. In Alaska, tamarack occurs throughout the river basins between the Brooks Range on the north and the Alaska Range on the south and is especially abundant along the Yukon, Kuskokwim, and Tanana Rivers (fig. 1) (Vioreck and Little 1975). During the same time period 70 percent of the tamarack trees in southeastern Yukon Territory were defoliated by *Z. improbana* (Walker) (Canadian Forestry Service 1976).

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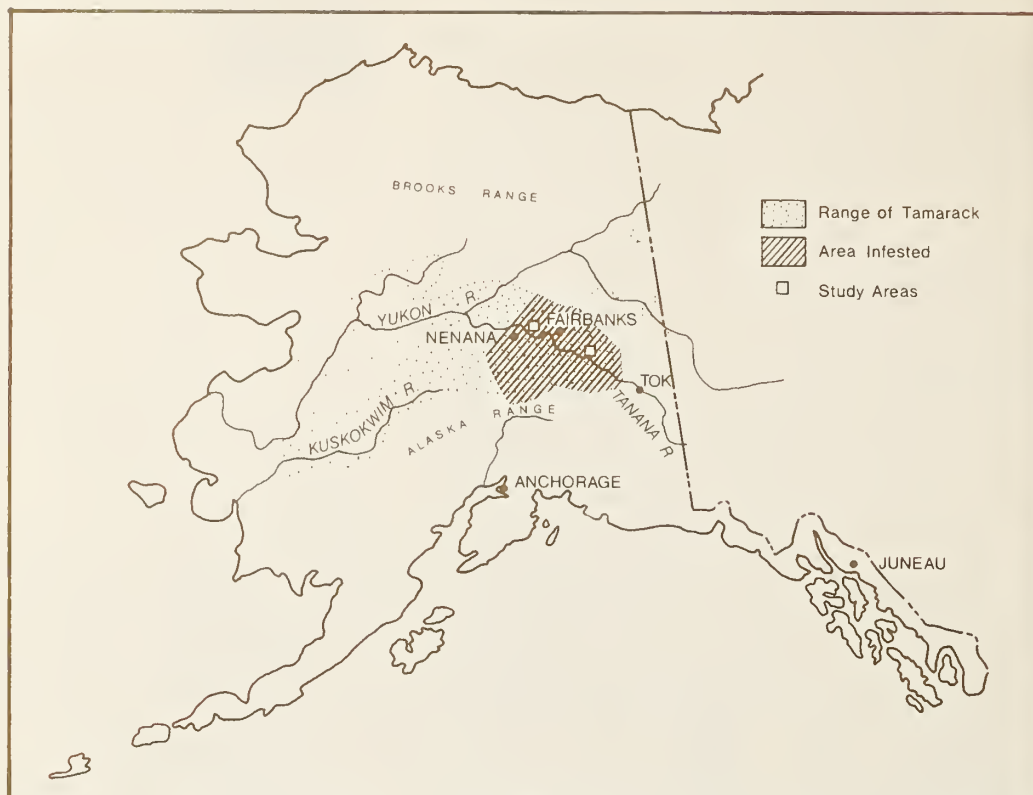


Figure 1.--Range of tamarack in Alaska and areas defoliated by larch bud moth, *Zeiraphera* sp.

Adult specimens reared during the 1975-1977 outbreak were identified by Dr. A. Mutuura, Biosystematics Research Institute, Ottawa, Ontario, as a possibly new species or subspecies of *Zeiraphera* closely related to *Z. improbana* (Walker). Mutuura and Freeman (1966) previously described seven North American species of *Zeiraphera*, and *Z. improbana* was the only species that fed on tamarack.

Baltensweiler et al. (1977) summarized the results of 26 years of research on the population dynamics of *Z. diniana* in Europe. The biology and behavior of the Alaskan species are quite similar to *Z. diniana* except for host plants. The Alaska *Zeiraphera* feeds predominantly on *L. laricina* whereas *Z. diniana* feeds on several different coniferous hosts.

This paper describes the life cycle and behavior of an unidentified species of *Zeiraphera* in tamarack stands of interior Alaska.

Methods

The study was conducted in two areas of heavy infestation located in the Tanana River drainage. Single sample plots were established in May 1975 in the Bonanza Creek Experimental Forest located 40 km west of Fairbanks and near Delta Junction located 134 km east of Fairbanks (fig. 1). The study sample plots contained open-grown, mixed species of tamarack and black spruce, Picea mariana (Mill.) B.S.P. The dominant and codominant trees ranged from ca. 6 to 9 m in height and ca. 6.5- to 15.2-cm d.b.h. Each of the two sample plots contained 100 trees which were marked and numbered with plastic tags. Branch samples were collected weekly from 10 randomly selected trees in each plot in order to estimate larval development and density from egg eclosion to pupation. All larvae were collected and counted on a 63-cm-long branch which was collected from the south side of the midcrown level. Preliminary sampling indicated no significant difference in egg or larval density in relation to crown level or direction. Larval density was expressed in terms of number per 0.64 m^2 ($1,000 \text{ in}^2$) of branch area.

Branches were clipped with a pole pruner equipped with a muslin basket lined with a plastic bag which in turn held the clipped branch. The plastic bag with branch was sealed and transported to the laboratory for processing. In addition, 200 larvae were collected each week and measurements made by ocular micrometer of body length and width and head capsule width. Other external characteristics such as color were examined.

Pupal development was measured by trapping last instars as they dropped from the trees. Wire screen traps (50- x 50- x 7.5-cm) were partially filled with peat moss covered with a 2.35-cm-thick layer of sphagnum moss and placed on the ground beneath infested larch. Escape of larvae from the traps was prevented by coating the upper surface of the wooden trap frame with Tanglefoot®.³ Pupal density was expressed as number per square meter. A wire screen cover was placed over the pupal trap following pupation in order to live trap emerging adult moths and parasites. Moth density and sex ratio were thus obtained. Pairs of adults were caged separately in plastic screen sleeve cages placed over the terminal 38 cm of uninfested tamarack branches. Mating and ovipositional behavior were observed and oviposition data recorded. Half of the sleeve cages were removed following oviposition in order to measure egg predation and parasitism.

All samples of larvae and pupae from the weekly collections were reared in the laboratory in order to collect emerging parasites. Diseased specimens were sent to specialists for identification.

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Description of Stages

Adults: Moths of both sexes have a grayish-black head, thorax, and abdomen with scattered patches of brown. Forewings are mottled grayish with patches of white, brown, and black scales. Hindwings are light gray with a fuscous fringe on the posterior edge. Adults are 7.3 ± 0.31 mm in length (range 6.2-10.8 mm) with a wingspread of 14.2 ± 0.6 mm (range 12.3-17.2 mm).

Egg: Eggs are oblong, ca. 0.35-0.60 mm in length and 0.15-0.25 mm in width. Color varied from whitish-orange immediately after oviposition, changing with age to a dullish reddish brown.

Larvae: Body and head capsule measurements and color variations are described for each instar in table 1. The thoracic legs of each instar are brown, but the head and body color varies. Newly emerged larvae are pale green with black heads and transform through successive instars to a fifth instar characterized by a brown head and yellowish green body with light brown dorsal and lateral spots.

Pupae: Pupae are dull brown and are found in cocoons constructed from forest floor materials such as peat, moss, bark scales, and bits of other plant material. Pupae are 11.1 ± 0.5 mm in length (range 9.5-12.6 mm) and 2.1 ± 0.1 mm in width (range 1.9-2.3 mm). Sexes can be separated according to location of the genital opening. Females have the opening ventrally on the eighth abdominal segment, whereas for males it occurs ventrally on the ninth segment.

Table 1--External measurements (mm) and color phases of larch bud moth, *Zeiraphera* sp., larvae collected from tamarack, Fairbanks, Alaska

Instar	I	II	III	IV	V
No. measured	200	250	350	325	340
Length:					
Mean	3.5	7.4	9.4	9.9	10.3
Range	2.8-4.2	5.3-9.2	8.2-10.7	7.0-11.5	8.7-12.8
Body width:					
Mean	0.51	0.72	1.12	1.18	1.75
Range	.47-.55	.66-.77	.82-1.23	.90-1.32	1.48-2.04
Head width:					
Mean	.50	.83	1.11	1.22	1.32
Range	.46-.54	.76-.96	1.06-1.16	1.18-1.26	1.28-1.40
Color:					
Head	black	black	brownish-black	dark brown	brown
Body	pale green	pale green	green	yellowish-green	yellowish-green

Life History and Behavior

The seasonal development of the larch bud moth in Alaska is shown in fig. 2. The bud moth is univoltine with an egg diapause. The factors responsible for the induction of diapause are unknown; however, diapause was terminated when temperatures reached 10°C. Overwintering eggs successfully survived temperatures as low as -52°C, which often occur in interior Alaska.

Adults emerged from late June until late July with peak flight occurring when cumulative degree days reached ca. 500° above a 5°C threshold usually in early July. Moth emergence occurred in the early morning between 0300 h and 0500 h when light intensity was ca. 700 lux and when daily temperatures were at a minimum (mean of 10°C in June and July). Flight and mating occurred at twilight (2250-0150 h). Twilight is that period when the sun is not more than 6° below the horizon (Johnson and Hartman 1969). At latitudes north of 60-1/2°N, evening twilight overlaps morning twilight during the summer. In the study areas there was ca. 3 h of twilight from late June to late July. The light intensity during this twilight period ranged from 13.5 lux at 2250 h and 0150 h to 8.6 lux at 2400 h.

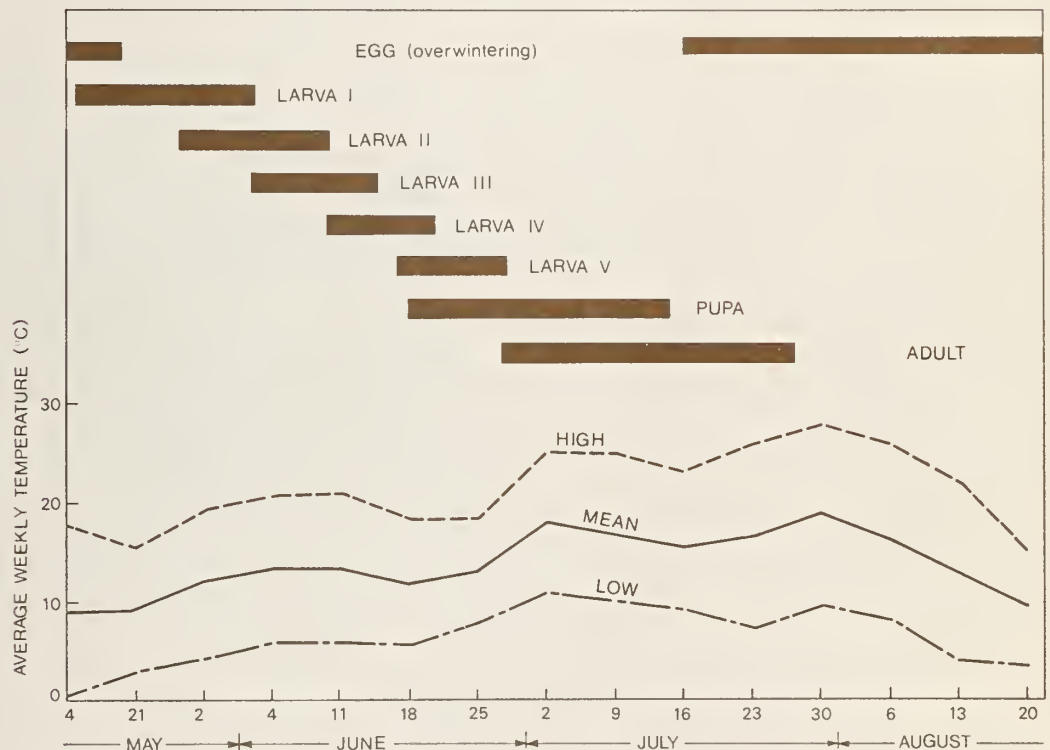


Figure 2.--Seasonal development of the larch bud moth, *Zeiraphera* sp., with daily temperatures in interior Alaska.

Mating occurred in previously defoliated trees which usually began to refoliate by mid-July. Adult females were capable of oviposition immediately after mating without a pre-oviposition period as was found with the spear-marked black moth, Rheumaptera hastata (L.), in Alaska (Werner 1977). Eggs were laid singly beneath bark scales, on cones, and in the axes of tree branchlets. An average of 160 eggs was laid per female over a period of 4 days.

First instars emerged in mid-May when the cumulative degree day temperature reached ca. 100° above the 5°C threshold. Larval emergence coincided with tamarack bud break, and thereafter larval development was closely related to host phenology. First instars fed within the newly developed needle clusters. Second, third, and fourth instars fed within a tubelike structure constructed from the needle clusters. Larval development began in mid-May and extended to mid-July. Fifth instars and occasionally fourth instars lived within finely webbed tunnels constructed along the branch axis. Fifth instars were often found outside of the webbed tunnels feeding on needles. Feeding by all instars except the first occurred during the twilight hours (2250-0150 h). First instar feeding occurred throughout all hours of the day.

When the fifth instars had completed feeding, they dropped to the ground on silken threads and constructed cocoons from pieces of moss, dead larch needles, or any other organic matter on the forest floor. The larvae did not burrow but followed natural channels in the peat soil which normally occurs beneath tamarack trees. Larvae preferred moist soil for pupation, and 80 percent of the cocoons were found within the upper 3 cm of the soil surface. Pupation began in late June and was completed by mid-July.

Natural Enemies

The impact of abiotic and biotic mortality agents on the density of the various stages of Zeiraphera sp. is shown in table 2. Rapid decreases in temperature during April 1976, i.e., from 0° to 30°C in 24 h, killed ca. 32 percent of the overwintering egg stage. Predation by lacewing larvae, Chrysopa sp., accounted for 2.4-percent reduction of the egg population following oviposition in July 1975 and the onset of winter in early October 1975. Predation by Chrysopa sp. and ants, Formica sp., reduced first-, second-, and third-instar populations by ca. 8 percent in 1975 and 9 percent in 1976. Bird predation removed 3 percent of the fourth instars and 10 percent of the fifth instars during the summers of 1975 and 1976. Slate-colored juncos, Junco hyemalis, redpolls, Acanthis sp., and chickadees, Parus sp., were observed feeding on larvae and adults.

Table 2--Seasonal density and mortality of Zeiraphera populations on heavy defoliation sites

Insect stage	Mean density ¹		Percent mortality	
	1975	1976	1975	1976
Egg (Sept.)	209+12.6	--	--	2.4
Egg (May)	--	123+10.2	31.6	--
Larvae I	112+8.5	94+9.6	1.3	2.1
Larva II	102+8.9	88+10.2	3.2	2.6
Larva III	75+6.3	68+8.4	3.8	3.2
Larva IV	72+4.5	63+5.6	4.9	12.2
Larva V	60+3.6	51+2.4	45.2	76.3
Pupa	89+1.3	43+1.7	62.3	99.6

¹Egg and larval density per 0.64 m² branch area. Pupal density per square meter of litter.

Parasitism accounted for 16-percent reduction of fifth instars in 1975 and 30 percent in 1976. The greatest impact of parasitoids was on the pupal stage with a 55-percent reduction in 1975 and a 90-percent reduction in 1976. Three species of braconids, Meteorus niveitarsis (Cress.), Apanteles sp., and Agathis sp. were reared from fifth instars. The following ichneumonids were reared from fifth-instar larvae: Glypta sp. and Elachertus sp.

Ichneumonid pupal parasitoids were Coccygomimus pedalis (Cress.), Mesochorus sp., Itoplectis quadricingulatus (Prov.), Gelis sp., and Mastrus annulicornis (Thom.). One tachnid Actia sp. was reared from late-instar larvae.

A granulosis virus contributed to a 24- to 31-percent decline of fifth instars in 1975 and 1976 and ca. 8-percent decline of pupae in both years. Dead and dying larvae were found in the webbed shelters along tamarack branches and hanging from foliage where they died while spinning to the ground to pupate.

Acknowledgment

Parasite identifications were made by taxonomists at the Biosystematics Research Institute, Ottawa, Ontario. Insect pathogens were determined by K. M. Hughes, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oregon. I am indebted to the biological technicians, especially Tom Egan and Tom Ward. Thanks are also due to reviewers of the manuscript: Dr. Akira Mutuura, Biosystematics Research Institute, Ottawa, Canada; Dr. Robert E. Stevens, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado; and Dr. Edward Holsten, USDA Forest Service, Anchorage, Alaska.

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Ectomycorrhizal Inoculation of Containerized Western Conifer Seedlings

Randy Molina¹

Abstract

Of 15 ectomycorrhizal fungi inoculated onto five container-grown conifer species (Larix occidentalis, Pinus contorta, P. ponderosa, Pseudotsuga menziesii, and Tsuga heterophylla), only Laccaria laccata and Cenococcum geophilum consistently formed ectomycorrhizae on all conifer hosts. Percents of mycorrhizal feeder roots were generally high, ranging from 86 on L. occidentalis to 94.5 percent on T. heterophylla for L. laccata and from 48.1 to 81.8 percent on these respective hosts for C. geophilum. L. laccata significantly colonized more feeder roots than C. geophilum for most conifer species. Only P. menziesii seedlings inoculated with C. geophilum were significantly larger than controls. There is a need for further studies with a wider range of fungi.

Keywords: Mycorrhizal inoculation, container nursery stock.

Introduction

Increasing needs to reforest cutover public and private forest lands have generated increasing demand for containerized seedlings. Given these needs as well as the sizable economic investments in container nurseries, use of container seedlings will continue for the immediate future.

Although the tops of seedlings grown in containers often grow luxuriantly, most root systems we have examined lack normal ectomycorrhizal development. This most likely results from the use of artificial (non-soil) potting substrates, restriction of natural fungus inoculation through greenhouse rearing, and, most importantly, the high dosages of regularly applied soluble fertilizers. High levels of fertility have been shown to retard mycorrhizal development of containerized seedlings (Marx and Barnett 1975). A more natural mycorrhizal root system may greatly improve planting success of containerized seedlings especially on hard-to-regenerate sites (Marx and Barnett 1975, Trappe 1977).

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Marx and Bryan (1975) have recently developed techniques to artificially inoculate bareroot seedlings with the ectomycorrhizal fungus Pisolithus tinctorius. Inoculations of containerized loblolly pine (Pinus taeda L.) (Marx and Barnett 1975, Ruehle and Marx 1977), lodgepole pine (Pinus contorta Dougl. ex Loud.) and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) (Molina 1979) by similar techniques have also been successful. Little data is available, however, on artificial inoculation with other ectomycorrhizal fungi. Trappe (1977) suggests that ectomycorrhizal fungi in the genera Rhizopogon and Suillus, with their ease of isolation and rapid growth in pure culture, offer high potential for artificial inoculation of conifer seedlings. Also, fungi in these genera often fruit only with a particular host genus or species; the more specialized, host-specific fungus may benefit its particular host more than would a non-host-specific fungus (Mikola 1970).

The purpose of this study was to assess the success of inoculating containerized Douglas-fir, western hemlock (Tsuga heterophylla (Raf.) Sarg.), western larch (Larix occidentalis Nutt.), lodgepole pine, and ponderosa pine (Pinus ponderosa Dougl. ex Laws.) seedlings with a variety of host specific and non-host-specific fungi and their effects on seedling growth.

Methods

Fungus Isolates

Table 1 lists the fungus isolates tested for each tree species and their dates of isolation. Except for Cenococcum geophilum, all had originally been isolated from sporocarp tissue; C. geophilum was isolated from a surface-sterilized sclerotium (Trappe 1969). All isolates were previously tested in pure culture synthesis to confirm their mycorrhiza-forming ability.

Inoculations with Laccaria laccata, Cenococcum geophilum, Pisolithus tinctorius, Paxillus involutus, and a control of no fungus addition served as common inoculation treatments for all tested host tree species. These fungi are well known for their broad host ranges (Trappe 1962). The remaining three to four fungi tested per host tree species (see table 1) were selected for their known or inferred specificity to that particular host.

Inoculum Preparation

Inoculum was prepared according to Marx and Bryan (1975) as modified by Molina (1979). Vegetative mycelium of each isolate was grown aseptically in glass-capped 2-liter flasks containing 1 450 ml of vermiculite plus 50 ml of sphagnum peat moss moistened with 750 ml of modified Melin-Norkrans nutrient solution (Marx 1969); dextrose was substituted for sucrose in this solution. Control flasks contained no fungus. After 3 months at room temperature, inoculum was removed from the flasks and leached with cold running tap water to remove unused nutrients. Excess free water was removed by gently squeezing the inoculum wrapped in cheesecloth. Inoculum was placed in plastic bags and stored overnight at 5°C.

Table 1--Ectomycorrhizal fungus isolates used to inoculate containerized western conifers and their dates of isolation

Tree species inoculated	No.	Fungus isolate	Date of isolation
		Species	
Douglas-fir and western hemlock	A-153	<u>Rhizopogon vinicolor</u> Smith	August 1975
	S-311	<u>Rhizopogon parksii</u> Smith	November 1976
	S-242	<u>Suillus ponderosus</u> Smith & Thiers	October 1976
	S-243	<u>Suillus lakei</u> (Murr.) Smith & Thiers	October 1976
Lodgepole and ponderosa pine	S-297	<u>Rhizopogon occidentalis</u> Zeller & Dodge	November 1976
	S-218	<u>Rhizopogon vulgaris</u> (Vitt.) M. Lange	September 1976
	S-223	<u>Suillus brevipes</u> (Pk.) Kuntze	September 1976
	S-222	<u>Suillus tomentosus</u> (Lanf.) Snell, Singer & Dick	September 1976
Western larch	S-255	<u>Suillus grevillei</u> (Kl.) Singer	October 1976
	S-281	<u>Fuscoboletinus aeruginascens</u> (Secr.) Pom. & Smith	October 1976
	S-298	<u>Suillus cavipes</u> (Opat.) Smith & Thiers	October 1976
All of the above	A-145	<u>Cenococcum geophilum</u> Fr.	December 1974
	S-238	<u>Laccaria laccata</u> (Scop. ex Fr.) Bk. and Br.	September 1976
	S-403	<u>Paxillus involutus</u> (Batsch.) Fr.	September 1977
	S-216	<u>Pisolithus tinctorius</u> (Pers.) Coker & Couch.	September 1976

Inoculation and Sowing

A potting substrate, containing equal volumes of vermiculite and sphagnum peat moss, was pasteurized in steam at 80°C for 30 min to kill resident mycorrhizal fungi. For each species of fungus, one part inoculum was added to six parts potting substrate in large plastic bags and was then vigorously shaken to evenly distribute the inoculum particles. Sixty individual "Leach super cell" containers, 165-ml capacity, were then filled with the inoculated potting substrate per tree-fungus combination; of these, groups of 20 cells each were then randomly placed into three replicate blocks per host tree. A randomized block design containing three replicate blocks, each with 20 seedlings per fungus treatment, was used for each tree species. The large number of treatment combinations necessitated keeping each tree species as a separate test. Cells were then sown with three prestratified seeds and misted twice daily until germination was complete. Seedlings were then thinned to one per cell.

Growing Conditions

All seedlings were grown in the greenhouse from late May through November 1978. Supplemental light of approximately 11 000 lx over a 15-h photoperiod was provided by overhead sodium-vapor lamps. Photoperiod was lengthened to 20 h from mid-August through September to offset premature budset. Because high fertility is known to retard mycorrhiza formation of container seedlings (Marx and Barnett 1975), a completely soluble 20-19-18 NPK fertilizer (Peat-lite special)² plus Sequestrene Fe 330 iron chelate were applied at approximately one-quarter strength, the dosage suggested by Owston (1975) for growing western conifers. The soluble fertilizer was dissolved in tap water and evenly distributed by hand over all seedlings at the rate of 6 g/m² of bench space; Sequestrene was applied at the rate of 3 g/m² of bench space. Each seedling thus received approximately 3.1 mg of Peat-lite special fertilizer plus 1.6 mg of Sequestrene in each fertilization. Fertilizations were performed twice monthly from July through October. Seedlings were mist irrigated with tap water as needed.

Data Collection and Analysis

At the end of the experiment, all seedlings were harvested and their roots gently washed free of potting substrate. Each seedling root system was examined by stereomicroscopy for success of inoculation. For those fungus treatments showing successful inoculation, 10 seedlings were randomly selected per treatment replication; and their height, stem diameter, percent of mycorrhizal feeder roots, and oven-dry weights of tops and

²Trade names used do not imply endorsement by the U.S. Department of Agriculture over similar products.

roots were recorded. Degree of mycorrhiza formation was assessed by randomly removing three to six major lateral roots per seedling from their points of attachment to the tap roots and then counting the total number of mycorrhizal and non-mycorrhizal feeder roots. At least 100 total feeder roots were counted per seedling. Mycorrhiza formation was expressed as percent of total feeder roots examined which had formed mycorrhizae. Control or inoculated seedlings with other, contaminant mycorrhiza types were discarded initially and not included in analyses. All results were subjected to analysis of variance and differences among treatment means were compared with Scheffé tests. All significant differences are reported at $P \leq 0.05$.

Results

Only 2 of the 15 fungi tested, L. laccata and C. geophilum, formed abundant mycorrhizae on all the conifer species. P. involutus produced mycorrhizae with only a few seedlings from each tree species. No mycorrhizae were produced by any Suillus species, Rhizopogon species, Fuscoboletinus aeruginascens, or P. tinctorius. Control seedlings were mostly free of any mycorrhiza formation. Thelephora terrestris (Ehrh.) Fr. was the most prevalent contaminant mycorrhizal fungus but only colonized about 4 percent of all seedlings.

Inoculation success with both L. laccata and C. geophilum was excellent. With very few exceptions, practically all L. laccata- and C. geophilum-inoculated seedlings formed abundant mycorrhizae. Percent of mycorrhizal feeder roots ranged from 86 on western larch to 94.5 percent on western hemlock for L. laccata inoculations and from 48.1 to 81.8 percent on these respective hosts for C. geophilum inoculations (table 2). Except for ponderosa pine, L. laccata significantly colonized more feeder roots than C. geophilum. Mycorrhizal development was always strongest at the top of seedling plugs for both fungi, but usually the entire plug was colonized.

L. laccata sporocarps fruited prolifically among the different hosts, and various stages of primordia were abundant in the containers. Sclerotia of C. geophilum were also frequently observed on the root systems. Both fungi were easily reisolated from these reproductive structures. The effects of these fungi on seedling growth will be briefly discussed for each tree species.

Douglas-Fir

L. laccata mycorrhizae were most often well developed, pinnately branched structures and averaged 89 percent of the total short roots. C. geophilum mycorrhizal development was also extensive, colonizing 76.7 percent of total short roots. Mycorrhizae were most often short and cylindric to simple pinnate and of typical jet black color.

Table 2--Mean growth and mycorrhiza formation of Douglas-fir, western hemlock, western larch, lodgepole pine, and ponderosa pine seedlings inoculated with Laccaria laccata and Cenococcum geophilum¹

Tree species	Fungus treatment	Height	Stem diameter	Dry weight		Top: root	Percent mycorrhizal short roots
				Tops	Roots		
		Centimeters	Millimeters	Grams			
Douglas-fir	Control	9.27a	2.00	0.535	0.921	0.585	--
	<u>Laccaria laccata</u>	9.20a	2.00	.549	.853	.656	89.0a
	<u>Cenococcum geophilum</u>	10.51b	2.02	.561	.813	.694	76.7b
Western hemlock	Control	12.23	2.09	.574	.581a	.996	--
	<u>Laccaria laccata</u>	11.44	1.94	.520	.489b	1.090	94.5a
	<u>Cenococcum geophilum</u>	12.56	1.96	.533	.474b	1.168	81.8b
Western larch	Control	9.97	2.17	.576	.679	.868ab	--
	<u>Laccaria laccata</u>	9.61	2.27	.468	.650	.735a	86.2a
	<u>Cenococcum geophilum</u>	12.08	2.03	.573	.626	.923b	48.1b
Lodgepole pine	Control	4.24	1.78a	.243	.670a	.360a	--
	<u>Laccaria laccata</u>	4.30	1.56b	.204	.501b	.418a	93.0a
	<u>Cenococcum geophilum</u>	4.42	1.77a	.274	.524ab	.532b	69.7b
Ponderosa pine	Control	5.84a	2.81a	.564a	.994a	.585	--
	<u>Laccaria laccata</u>	5.27a	2.24b	.319b	.607b	.557	89.5
	<u>Cenococcum geophilum</u>	5.81a	2.45ab	.499ab	.740b	.684	77.8

¹When no letters follow a group of means, no significant differences were seen in the analysis of variance. Means within individual tree species not sharing a common letter are significantly different ($P \leq 0.05$) by Scheffe tests.